



Haddock

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On the cover: Haddock, Melanogrammus aeglefinus. Photograph by Robert K. Brigham, BCF.



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A Review of Stock Identification of Haddock, *Melanogrammus aeglefinus*, in the Northwest Atlantic Ocean

GAVIN A. BEGG

Introduction

Haddock, Melanogrammus aeglefinus (Fig. 1), is a commercially important groundfish species of the gadid family that is distributed throughout the northwest Atlantic from Greenland to Cape Hatteras (Bigelow and Schroeder, 1953). This range is effectively divided by the Fundian ("Northeast") and Laurentian Channels, both in excess of 180 m in depth (Fig. 2). Although had-

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ABSTRACT-Haddock, Melanogrammus aeglefinus, is a principal commercial species distributed throughout the northwest Atlantic Ocean, with major aggregations occurring on Georges Bank and on the Scotian Shelf. This review examines all available information on stock structure of haddock to evaluate the suitability of current stock units and to investigate areas that require further research. Combined information from tag-recapture, demographic, recruitment, meristic, parasitic, and genetic studies provide evidence for the identification of haddock stocks, with major population divisions occurring between New England, Nova Scotia, and Newfoundland waters. Within each of these major divisions a number of discrete stocks appear to exist, although uncertainty remains in the amount of separation found within each region. Research utilizing more recent stock identification techniques should refine and improve our understanding of haddock stock structure in the northwest Atlantic.

dock are demersal, they are rarely found in abundance below 180 m, resulting in the channels acting as barriers to dispersal (Needler, 1930). Haddock are found in cool, temperate waters across the continental shelf and over offshore submerged banks, with major commercial aggregations occurring on the southern Grand Bank, Scotian Shelf, and Georges Bank (Zwanenburg et al., 1992).

Historically, haddock has been a key species in terms of abundance and contribution to the commercial fisheries in the northwest Atlantic with peak landings of 249,000 metric tons (t) in 1965 (ICNAF, 1967). In contrast, landings have declined to 24,500 t in 1992 (NAFO, 1995), with most haddock stocks across the region in a depressed condition and the focus of rebuilding plans (Fig. 3) (Murphy and Bishop, 1995; Hurley et

al., 1997; Frank et al., 1997; Gavaris and Van Eeckhaute, 1998; Brown¹).

Beneficial to stock recovery and effective fisheries management is the "stock concept," as recruitment within each stock must sustain each population's catch (Kutkuhn, 1981). In fisheries science, many claim that the most useful definition of a stock is one that has a sound genetic basis because management policies may not achieve long-term conservation goals without the knowledge of the number of noninter-breeding, self-recruiting populations contained within an exploited species distribution (Ovenden, 1990). Similarly, in accordance with the "biological stock

¹ Brown, R. W. 1998. U.S. assessment of the Georges Bank (5Z) haddock stock, 1998. U.S. Dep. Commer, NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent., NEFSC Lab. Ref. Doc. 98.

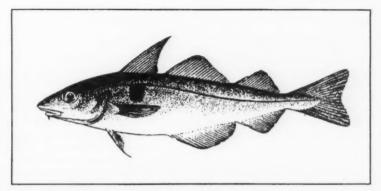


Figure 1.—Haddock, Melanogrammus aeglefinus.

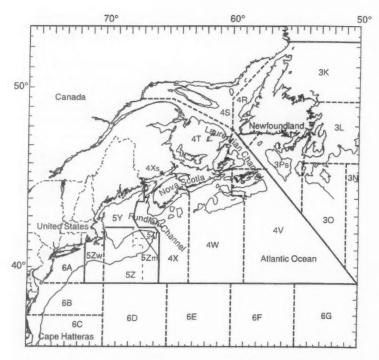


Figure 2.—ICNAF/NAFO scientific and statistical subareas, divisions, and subdivisions of the northwest Atlantic.

concept," fisheries management in the northwest Atlantic has been concerned with the delineation of fishing areas that correspond to geographic ranges of independently reproducing populations (stock distribution areas) (Zwanenburg et al., 1992). Interpretation of stock structure in this review relates to the lhssen et al. (1981) definition of a stock as "a group of randomly mating, reproductively isolated individuals of a single species with temporal or spatial integrity."

The definition of management units in the northwest Atlantic upon which haddock stocks are assessed and regulated has been based not only on considerations of biological stock structure, but also on considerations of other species and fishery distributions, oceanographic features, submarine topography, political and administrative boundaries, homogeneity of international fisheries participation, and practicalities of data collection and fishery regulation (Halliday and Pinhorn, 1990). In contrast to biological stock units, fisheries manage-

ment units are geographic areas in which a suite of regulatory measures can be applied to achieve specific management objectives (Gavaris and Van Eeckhaute, 1998). Currently, six stocks are recognized for haddock in the northwest Atlantic: 1) Grand Banks (Div. 3LNO), 2) St. Pierre Bank (Div. 3Ps), 3) Eastern Scotian Shelf and Southern Gulf of St. Lawrence (Div. 4TVW), 4) Western Scotian Shelf (Div. 4X), 5) Georges Bank (Div. 5Zjm - Canada; Div. 5Z - USA), and 6) Gulf of Maine (Div. 5Y) (Fig. 2).

Stock identification studies of haddock in the northwest Atlantic have been conducted since the 1930's, using a variety of approaches including tagrecapture, demographic, recruitment, meristic, parasitic, and genetic techniques. Delineation of haddock stocks has been complicated by seasonal differences in the species' spatial distributions (Zwanenburg et al., 1992) and the limitations associated with individual stock identification methods. This pa-

per reviews the literature on stock identification of haddock in the northwest Atlantic in order to evaluate the suitability of the current management/stock units by using all available biological information, rather than that acquired from a single procedure in isolation. Areas for future research are also discussed.

Stock Identification Techniques

Tag-Recapture

Stock identification of haddock in the Gulf of Maine and Nova Scotian waters was initially determined using tagrecapture methods (Needler, 1930; Schroeder, 1942; McCracken, 1960; Halliday and McCracken, 1970; Mc-Kenzie²; McCracken³). Needler (1930) hypothesized three main stocks of haddock in the northwest Atlantic (New England, Nova Scotia, and Newfoundland) based on divisions of shallowwater areas by the Fundian and Laurentian Channels and movement patterns of the species. Tag-recapture data have indicated that there is little interchange between haddock from New England and Nova Scotian waters (Fig. 4, 5) (Needler, 1930; Schroeder, 1942). However, in the Bay of Fundy, where the two regions are linked by shallow water, some mixing of haddock occurs (Fig. 6) (Needler, 1930; McCracken, 1960; Halliday and McCracken, 1970).

Seasonal migrations have been observed in haddock from both New England and Nova Scotian waters (Needler, 1930: McCracken, 1960: Halliday and McCracken, 1970). Typically, haddock move to inshore shallow waters in spring and to deeper offshore waters throughout winter and late summer (Fig. 6) (Needler, 1930). A large number of local tag-returns a year or more later show that most haddock return to the same locality (Needler, 1930). Tagrecapture data have indicated that a separate seasonally migrating stock exists along the coast of the Gulf of Maine from Jeffreys Ledge to the Bay of

² McKenzie, R. A. 1940. The spring haddock "run," Jordan Harbour, N.S. Fish. Res. Board Can., Atl. Prog. Rep. 28:9-13.

³ McCracken, F. D. 1956, Cod and haddock tagging off Lockeport, N.S. Fish. Res. Board Can., Atl. Prog. Rep. 64:10-15.

Fundy (Div. 5Y/4Xs) (Schroeder, 1942: Grosslein, 1962). McCracken (1960) observed a northward migration of haddock in the Gulf of Maine in spring. followed by a return migration in winter, with some recaptures on Georges Bank and across the Bay of Fundy. Likewise, in waters of eastern Nova Scotia there is evidence that haddock summer in the north and winter in the south, with a seasonal migration in and out of the Gulf of St. Lawrence (Div. 4TVW), although these patterns were based almost exclusively on the results of inshore tagging studies and recaptures from mainly inshore fisheries (Fig. 4) (Needler, 1930). Tag-recapture data also suggest that much of the stock present in summer along the coast of western Nova Scotia (Div. 4X) move offshore in autumn to Browns Bank and return the following spring (Fig. 6) (Halliday and McCracken, 1970). In contrast, a more recent tagging study by Zwanenburg4 found that there was no evidence for seasonal migrations of haddock tagged on offshore banks in Division 4TVW, with the results indicating that these fish are relatively sedentary.

Similarly, resident stocks of haddock are found year round which do not appear to participate in such seasonal migrations (Schroeder, 1942; Halliday and McCracken, 1970). A relatively nonmigratory stock appears to remain localized around the Great South Channel-Nantucket Shoals region (Grosslein, 1962), although some of the stock may participate in seasonal migrations to the Bay of Fundy and Georges Bank (Schroeder, 1942). Likewise, when a large proportion of the stock along the western coast of Nova Scotia migrates to neighboring offshore banks, a resident inshore stock appears to remain there throughout the winter (Halliday and McCracken, 1970).

Results from the different tagging studies have shown that major stock divisions occur between haddock from New England and Nova Scotian waters.

Figure 3.—Historical commercial catches (1,000 t) by stock division (Murphy and Bishop, 1995; Frank et al., 1997; Hurley et al., 1997; Brown, text footnote 1).

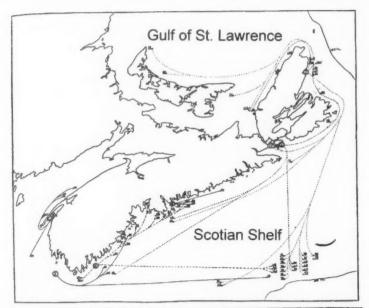
But how much interchange there is between haddock stocks from bank to bank or between inshore and offshore fishing grounds has not been answered by the various studies (Schroeder, 1942), although they have indicated that stock division probably does occur within each of the major regions. Also, it is difficult to discern from the tagging studies how much of the movements are seasonal migrations of more or less distinct stocks, and how much interchange there is between these stocks (Needler, 1930). Tagging of haddock has generally occurred through-

out spring and summer and has been restricted to inshore waters, with very few fish tagged offshore, except for the more recent study by Zwanenburg.⁴ Consequently, the patterns proposed by the earlier researchers may have been the results of examining a limited data set which described the movements of then extant inshore stocks of haddock (Zwanenburg⁵). Movement patterns

Div. 5Z Div. 5Y 160 12 120 9 Catch (1,000 t) Catch (1,000 t) 80-6 40 3 0 0 1950 1960 1970 1980 1990 2000 1950 1960 1970 1980 1990 2000 Year Year Div. 4TVW Div. 4X 60 32 Catch (1,000 t) 45 Catch (1,000 t) 24 30 16 15 8 0 0 1950 1960 1970 1980 1990 2000 1950 1960 1970 1980 1990 2000 Year Year Div. 3LNO Div. 3Ps 80 60 Catch (1,000 t) Catch (1,000 t) 60 45 40 30 20 15 to promote 0 0 1950 1960 1970 1980 1990 2000 1950 1960 1970 1980 1990 2000 Year Year

⁴ Zwanenburg, K. C. T. 1987. Marine Fish Division, Bedford Institute of Oceanography, P. O. Box 1006, Dartmouth, N.S., Can., B2Y 4A2. Unpubl. data on file at the Bedford Institute of Oceanography.

⁵ Zwanenburg, K. C. T. 1998. Marine Fish Division, Bedford Institute of Oceanography, P. O. Box 1006, Dartmouth, N.S., Can., B2Y 4A2. Personal commun.



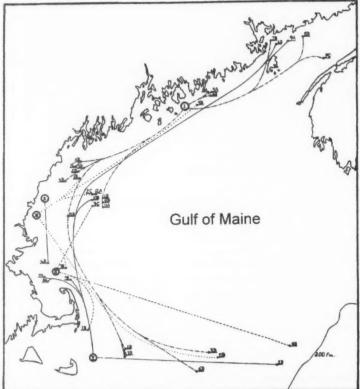


Figure 4.—Migration patterns of tagged haddock in New England and Nova Scotian waters showing little exchange between tagged fish in the two regions (Needler, 1930).

presented by the recaptures, therefore, is incomplete and may be biased by variable fishing effort. Also, the present patterns of distribution and movement may be difficult to compare to previous work in that the earlier population levels are so different from present very low levels (Zwanenburg⁵).

Demographics

Demographic or biological population parameters have been used to differentiate a finer scale of haddock stock separation in northwest Atlantic waters than that achieved by tag-recapture practices (Table 1). Growth differences of haddock from New England and Nova Scotian waters support the current stock units throughout these regions (Fig. 7). Needler (1930) observed differences in growth rates of haddock from corresponding inshore and offshore areas of New England and Nova Scotia, providing further evidence to the tag-recapture data of stock division between fish from these regions. Inshore Gulf of Maine (Div. 5Y) and offshore Georges Bank (Div. 5Z) haddock grew faster than those in coastal Nova Scotian waters and Browns Bank, respectively (Div. 4X), Likewise, Schuck and Arnold (1951) found significant differences in mean length-at-age between haddock from Georges Bank and Browns Bank, suggesting that little mixing occurs between fish from these regions.

As suggested by the tagging studies, stock structure was also apparent within each of the major regions, with the possibility of distinct inshore and offshore stocks. Haddock along the coast of the Gulf of Maine appear to grow slower than those fish from Nantucket Shoals and Georges Bank, indicating possible stock division between fish from these areas (Clark et al., 1982; Begg et al.6). Differential growth rates between haddock from the eastern part of Georges Bank and Nantucket Shoals suggested that fish from these areas may also be distinct stocks (Begg et al.6). Similarly, faster growth rates of inshore haddock than those from offshore waters of the

⁶ Begg, G. A., J. A. Hare, and D. D. Sheehan. The role of life history parameters as indicators of stock structure. Manuscr. in review.

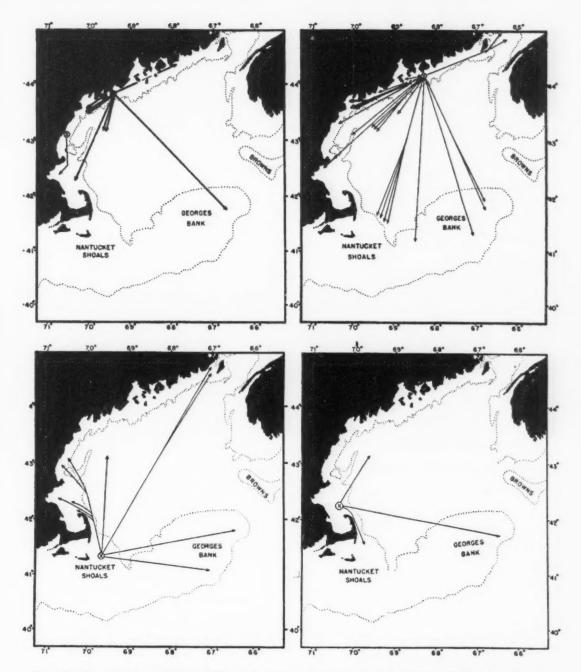


Figure 5.—Migration patterns of tagged haddock in New England waters, showing little exchange with Nova Scotian stocks, except in the Bay of Fundy (Schroeder, 1942).

Scotian Shelf suggested stock division Hennemuth et al. (1964) observed simiwithin this region (Needler, 1930).

haddock from the western (Div. 4X) and lar growth rates and age composition of eastern (Div. 4VW) part of the Scotian Shelf and the southern Gulf of St. Lawrence (Div. 4T). In contrast, haddock in the Bay of Fundy (Div. 4Xs) had a faster growth rate and younger age composition than those from waters off western Nova Scotia (Hennemuth et al., 1964), although these differences may have been influenced by gear selectivity problems and mixing of haddock from New England and Nova Scotian

Recaptures Dec. - May '57 + '58

Tagged Passamaquoddy Bay Tagged Digby Neck stocks within the bay. Beacham (1983) and Trippel et al. (1997) found differences in median lengths at sexual maturity among haddock from eastern and western Scotian Shelf waters, although these results were not statistically compared (Table 1). Haddock from the western Scotian Shelf (Div. 4X) tend to be larger and older at maturation than those from Georges Bank (Div. 5Z) (Over-

holtz, 1987), but smaller than those from St. Pierre Bank (Div. 3Ps) (Table 1). Stock separation of haddock within Newfoundland waters has been based mainly on differences in growth rates (Templeman et al., 1978a). Haddock on St. Pierre Bank typically grow faster and are of a greater mean length-at-age and length at first-maturity than those on the Grand Bank (Div. 3LNO) (Table 1) (Templeman et al., 1978a,b; Templeman and Bishop, 1979a,b).

Stock division of haddock inferred from several demographic characteristics has tended to agree with patterns developed from the tag-recapture studies. However, for the most part, individual regional growth curves have not been compared in a statistically rigorous fashion to determine the significance, if any, of the apparent growth differences used to separate the stocks (Schuck and Arnold, 1951). Needler (1930) only presented average lengthat-age data, and samples were taken by commercial fishing gear which excluded younger haddock, while probably selecting for larger sizes of specific aged fish. Consequently, discrepancies in growth rates estimated by Needler (1930) and Hennemuth et al. (1964) may have been related to differences in sampling and analytical methodologies. Differences in sampling times and gear types between the various studies has resulted in a lack of homogeneity in the origin of the samples used to provide demographic characters to differentiate haddock stocks. Also,

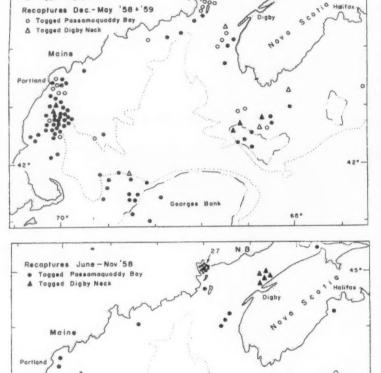


Figure 6.—Seasonal migrations of haddock in New England and Nova Scotian waters, tagged along the eastern and western shores of the Bay of Fundy (McCracken, 1960).

Browns

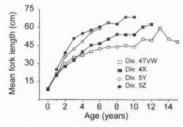


Figure 7.—Growth differences in mean lengths at age among haddock stocks Div. 4TVW (Frank et al., 1997), 4X (Hurley et al., 1997), 5Y and 5Z (calculated from 1997 NMFS Northeast Fisheries Science Center spring bottom-trawl survey data).

while the magnitude of the differences in growth rates that have been detected among haddock from some regions may be sufficiently large to indicate real differences in the stocks (Hennemuth et al., 1964), these differences may be the result of demographic plasticity within stocks as a response to changing ambient abiotic and biotic conditions.

Spawning and Recruitment Patterns

Spawning Times and Locations

Further evidence for stock discrimination of haddock within New England and Nova Scotian waters has been provided by spawning and recruitment patterns of the species in relation to the distinct oceanographic conditions of each region. Peak spawning of haddock occurs in late March and early April within New England (Marak and Livingstone, 1970; Grosslein and Hennemuth, 1973; Lough and Bolz, 1989), from late April to June in Nova Scotia (Hurley and Campana, 1989; Page and Frank, 1989; Waiwood and Buzeta, 1989), and throughout June and July in Newfoundland waters (Templeman et al., 1978b; Templeman and Bishop, 1979b). Spawning periodicity of haddock is highly variable and appears to be correlated with water temperature, resulting in delayed spawning during colder years and advanced spawning during warmer years (Page and Frank, 1989).

Throughout the northwest Atlantic the main spawning grounds of haddock occur over Georges Bank (Div. 5Z), the western part of the Scotian Shelf (Div. 4X), Gulf of Maine (Div. 5Y), Nantucket Shoals (Div. 5Z), Emerald-Western Banks (Div. 4VW), Grand Bank (Div. 3LNO), and St. Pierre Bank (Div. 3Ps) (Fig. 8) (Colton and Temple, 1961; Smith and Morse, 1985; Page and Frank, 1989). Along the Scotian Shelf the primary spawning grounds occur on Browns Bank (Div. 4X) and Emerald-Western Banks (Div. 4VW), with lower levels on adjacent banks and in inshore coastal areas (Hurley and Campana, 1989; Campana et al., 1989). Buoyancy characteristics of haddock eggs and local physical and oceanographic conditions may result in hatching failure throughout these inshore waters (Frank

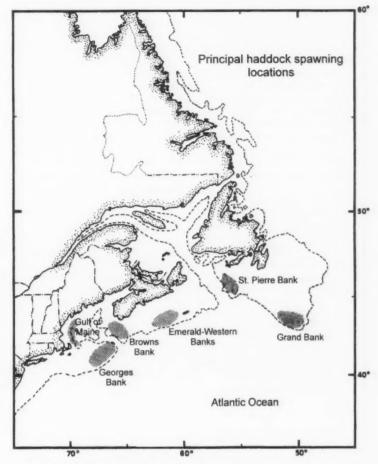


Figure 8.—Principal spawning locations of haddock in the northwest Atlantic (Page and Frank, 1989).

Table 1.—Summary of biological parameters (length/age at 50% maturity: $L_{\rm so}$, $A_{\rm so}$; and von 8 coefficients: $L_{\rm co}$, K, $t_{\rm o}$) derived for each haddock stock Div. 3LNO, 3Ps, 4TVW, 4X, 5Y, and 5Z. a: and von Bertalanffy growth

Parameter	Stock division					
	3LNO	3Ps	4TVW	4X	5Y	5Z
L _{so} (cm) females	511	503	304	384	39 ⁷	397
L _{so} (cm) males	441	403	294	334	277	317
A _{so} (years) females	5.11	4.33	3.44	3.64	2.87	2.47
A _{so} (years) males	4.01	3.33	2.94	3.34	1.97	1.87
L _{oo}	74.82	84.62	51.35	76.66	72.98	73.88
K	0.102	0.242	0.265	1.126	0.358	0.388
t _o	-3.62	0.472	-0.975	0.186	0.308	0.178

Templeman et al. (1978b).

Templeman and Bishop (1979a).

Templeman and Bishop (1979b).

Trippel et al. (1997).

Calculated from mean lengths-at-age reported in Frank et al. (1997).

O'Boyle et al. (1988).

Begg et al., text footnote 6

O'Brien et al. (1993).

et al., 1989). Significant spawning also occurs on the southwestern portion of Banquereau Bank, but this appears to occur only during high population density and as such may represent spillover from the Emerald-Western spawning grounds (Zwanenburg⁵). Spawning of haddock occurs near the substratum during spring when the water column is beginning to stratify, resulting in the eggs floating to the surface (Walford, 1938). Although eggs in early stages of development are concentrated in the surface layers, the proportion in deeper waters increases as eggs develop. thereby reducing the effects of winddriven transport in dispersal from the spawning grounds (Page et al., 1989).

Retention of Spawning Products

Surface circulation patterns within New England waters are dominated by seasonally variable gyres that are counterclockwise in the Gulf of Maine and clockwise on Georges Bank (Fig. 9) (O'Boyle et al., 1984; Loder et al., 1988; Drinkwater, 1996). These patterns tend to retain eggs and larvae in the areas from which they originate. Larvae originating on Georges Bank are transported in a westerly direction, but are mostly retained on the bank that acts as both a spawning and nursery area (Grosslein and Hennemuth, 1973; Sherman et al., 1984; Smith and Morse, 1985; Lough and Bolz, 1989). Larvae that are spawned on the northeast section of Georges Bank during spring have a continuous recruitment to the central part of the bank as they develop and are advected there along its southern flank (Lough and Bolz, 1989). However, transport of larvae off Georges Bank can occur due to unusually strong geostrophic currents, such as in the spring of 1987, with sufficient magnitude to

be an important factor influencing the stock composition of neighboring southwesterly regions, such as Nantucket Shoals (Polacheck et al., 1992). Most of the larvae associated with the outside of the Georges Bank gyre pass south of the Great South Channel, where no evidence of significant spawning has been detected, and settle throughout the Nantucket Shoals region (Smith and Morse, 1985).

Likewise, on the Scotian Shelf distributions of haddock larvae are associated with gyres that tend to concentrate and maintain spawning products over relatively shallow banks of the shelf, thereby playing a functional role in maintenance of stock integrity (Fig. 10) (O'Boyle et al., 1984; Smith, 1989). Campana et al. (1989) proposed that drift and retention processes operate together on the permanent, tidally induced, clockwise gyre around Browns

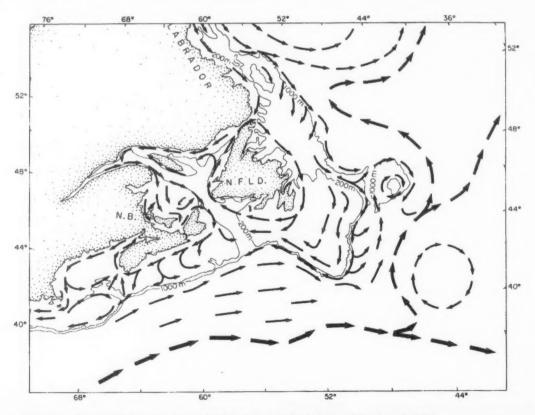


Figure 9.—General circulation patterns within the northwest Atlantic Ocean (O'Boyle et al., 1984).

Bank to retain some larvae on the bank, while transporting others towards inshore waters and to the Bay of Fundy. creating a single retention zone or unit stock throughout this region (Div. 4X). Although larvae are retained on the western banks of Nova Scotia, the same does not appear to occur on most of the eastern banks, which may be explained by the existence of gyres in the former areas acting as larval entrainment mechanisms (O'Boyle et al., 1984). Frank (1992) proposed a density-dependent dispersive model for haddock stocks in these waters, where he suggested juvenile haddock of strong year classes disperse from their spawning grounds in Division 4VW to those in Division 4X, thereby supplementing and assisting in the stability of the stock in Division 4X.

Smith and Morse (1985) found that haddock eggs and larvae originating on Georges Bank, Gulf of Maine, and Scotian Shelf spawning grounds do not intermix, and hence, are geographically isolated and constitute separate stocks. On Georges Bank, two spawning aggregations appear to exist with one on the Northeast Peak ("Eastern Georges Bank") and the other around Nantucket Shoals ("Western Georges Bank") (Fig. 11). The depth and strong currents associated with the Fundian Channel provides a natural boundary for separating spawning products from Georges Bank and the Scotian Shelf spawning grounds. Likewise, the broad, deep central basin of the Gulf of Maine may isolate eggs and larvae on the Scotian Shelf from those in coastal New England waters (Smith and Morse, 1985). Little evidence of ichthyoplankton exchange between Georges and Browns Banks supports the hypothesis of isolation and maintenance of distinct stocks of haddock within these regions (Hurley and Campana, 1989). Similarly, data from the NMFS Northeast Fisheries Science Center spring bottom-trawl surveys, 1988-97, indicate a relatively discontinuous distribution of haddock spawning aggregations (Georges Bank, Nantucket Shoals, Gulf of Maine, Browns Bank, and along the inshore western Scotian Shelf) (Fig. 11).

Synchrony of Recruitment

Interrelationships may exist between haddock stocks throughout the Gulf of Maine, Georges Bank, Nantucket Shoals, and Browns Bank, as the same year classes have historically tended to show similar patterns in recruitment throughout this entire region (Clark et al., 1982; Koslow, 1984; Koslow et al., 1987; Thompson and Page, 1989). Recent studies have suggested large-scale physical and biological forcing are partly responsible for synchrony in recruitment and year-class success among different stocks (Koslow, 1984; Koslow et al., 1987). However, Cohen et al. (1991) indicated local-scale processes, rather than large-scale physical forcing. dominate recruitment patterns, because

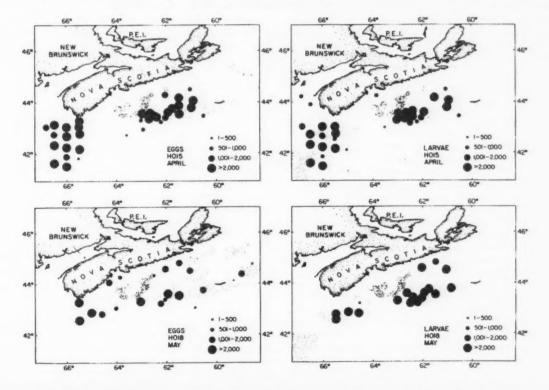


Figure 10.—Spatial and temporal distributions of haddock eggs and larvae on the Scotian Shelf (O'Boyle et al., 1984).

most significant correlations were found between neighboring stocks.

Meristics and Morphometrics

Meristic characters, in the form of vertebral number, have been used to provide insights into stock structure of haddock (Clark and Vladykov, 1960; Tremblay et al., 1984; Vladykov⁷). Vladykov⁷ used vertebral counts of adult haddock to confirm the three population groups suggested by Needler (1930): New England, Nova Scotia, and Newfoundland. After updating this meristic analysis, Clark and Vladykov (1960) proposed that the Nova Scotia stock be divided into three stocks: eastern, central, and western Nova Scotia. Mean number of vertebrae differed significantly between the five stocks and increased with latitude from New England to the eastern Scotian Shelf, suggesting an inverse relationship with water temperature (Fig. 12). In contrast, Tremblay et al. (1984) found lower vertebral numbers for juvenile haddock from the northeastern part of the Scotian Shelf (Div. 4V) than those from central (Div. 4W) and western Nova Scotian waters (Div 4X). Based on these differences, they proposed that the haddock stock occupying the northeastern and central area (Div. 4VW) of the Scotian Shelf be divided into two stock components: eastern Scotian Shelf (Div. 4V) and central Scotian Shelf (Div. 4W).

A major limitation of these meristic studies has been the lack of temporal comparisons to examine the consistency of stock structure patterns over time. Spatial comparisons have also been restricted, with few inshore samples having been collected. Results presented by Tremblay et al. (1984) were mean values and were not accompanied by data showing the amount of variability both within and between samples. Consequently, it is difficult to comment on the validity of the differences in their results compared to those of Clark and Vladykov (1960). The actual degree of mixing between stocks cannot be estimated from any of the meristic studies, and the minor differences used to sepa-

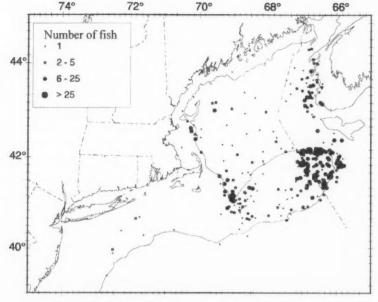


Figure 11.—NMFS Northeast Fisheries Science Center spring bottom-trawl survey catch (number) per tow of sexually mature haddock, 1988–97.

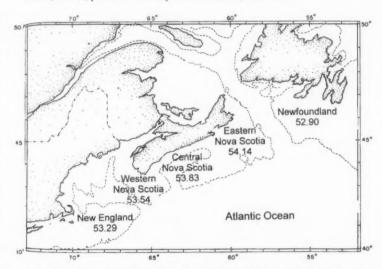


Figure 12.—Mean vertebrae number of haddock from fishing grounds of the northwest Atlantic Ocean (Clark and Vladykov, 1960).

rate stocks should be viewed with caution, particularly given the high degree of environmentally influenced plasticity that can exist in meristic characters.

More recently, otolith shape analysis was investigated to determine its utility as a tool for stock discrimination of haddock stocks in the northwest Atlantic (Begg⁸). Several shape variables

⁷ Vladykov, V. D. 1935. Haddock races along the North American coast. Biol. Board Can., Atl. Prog. Rep. 14:3-7.

⁸ Begg, G. A. 1998. Northeast Fisheries Science Center, National Marine Fisheries Service, NOAA, 166 Water Street, Woods Hole, MA 02543. Unpublished data on file at the Northeast Fisheries Science Center.

were statistically significant between haddock samples from Georges Bank, the Gulf of Maine, and the Scotian Shelf, providing a phenotypic measure of stock separation.

Parasites

The use of parasites for stock identification of haddock in the northwest Atlantic has been limited to a preliminary study by Scott (1981). A total of 19 species of alimentary-tract parasites of haddock from the Scotian Shelf were identified, although most of them were ubiquitous, occurring in a variety of hosts over wide geographical areas. Only two species (Digenea: Lepidapedon rachion and Myxosporida: Myxidium bergense) showed the degree of host specificity, abundance, and correlation with known haddock stock delineation needed to be considered prospects for biological tags. Infestation of L. rachion in haddock from Browns Bank (Div. 4X) was higher than those from the Bay of Fundy (Div. 4Xs) and lower than those from the Emerald-Banquereau area (Div. 4W), providing indirect evidence for separate stocks in these areas (Scott, 1981). Of interest is that parasites have been used successfully to distinguish haddock stocks in the northeast Atlantic. Lubieniecki (1977) analyzed the incidence and intensity of infestation with Grillotia erinaceus plerocerci to indicate a number of separate stocks of haddock within this region. In contrast, Scott (1981) found that G. erinaceus was not a major parasite in haddock from the northwest Atlantic, thereby reducing its utility as a biological tag in these waters.

Genetics

Genetic information obtained from mitochondrial DNA procedures has not been considered in construction of the present management units of haddock stock structure in the northwest Atlantic (Zwanenburg et al., 1992), although genetically discrete stocks have been identified using electrophoretic techniques in northeastern Atlantic waters (Jamieson and Birley, 1988). Importantly, the stock structure of haddock identified by the genetic results of Jamieson and Birley (1988) was con-

Table 2.—Results of stock identification studies to differentiate haddock stocks in the Northwest Atlantic.1

	Stock structure (no. of stocks identified within)			
Stock I.D. method	New England	Nova Scotia	Newfoundland	
Tag-recapture	1-2 (5Y; 5Z / N.Sh.?)	2 (4X: 4TVW)	N/A	
Growth rates	2-3 (5Y; 5Z; N.Sh.?)	(4X: 4TVW)	(3Ps; 3LNO)	
Spawning patterns	2-3 (5Y; 5Z; N.Sh.?)	2 (4X: 4TVW)	2 (3Ps: 3LNO)	
Meristics	N/A	3-4 (4X; 4V; 4W; 4T?)	N/A	
Parasites	N/A	3 (4Xs: 4X: 4W)	N/A	
Genetics	?	?	N/A	
Current management units	1(Canada) / 2 (USA) (5Zjm - Canada; 5Z, 5Y-USA)	(4X; 4TVW)	(3Ps; 3LNO)	

¹ Key: Div. 5Z|m - Georges Bank, Canada; Div. 5Z - Georges Bank, USA; Div. 5Y - Gulf of Maine; N.Sh. - Nantucket Shoals; Div. 4X - Western Nova Scotia; Div. 4Xs - Bay of Fundy; Div. 4W - Central Nova Scotia; Div. 4V - Eastern Nova Scotia; Div. 4T - Gulf of St. Lawrence; Div. 3Ps - St. Pierre Bank; Div. 3LNO - Grand Bank, N/A = No data available. ? = Results uncertain.

sistent with the parasitic study of Lubieniecki (1977).

Examination of mitochondrial DNA in haddock from the northwest Atlantic has provided conflicting information on the stock structure of the species in this region. Zwanenburg et al. (1992) determined that haddock sampled from offshore banks of New England (Georges, Div. 5Z), Nova Scotia (Browns, Div. 4X; Western, Div. 4W; Banquereau, Div. 4V), and Newfoundland (St. Pierre. Div. 3Ps) were comprised of a mixture of divergent genotypes that may have arisen in past populations that were more isolated than those at present. Although, no statistically significant differences in pair-wise comparisons of genotype frequencies among haddock from any of the banks were detected, gene flow among the population was considered to be restricted. A geographic cline in genotype frequency, increasing genetic differences with geographic distance (Fig. 13), and the deep ocean channels acting as barriers to gene flow formed the basis for their reasoning of stock separation. In contrast, Purcell et al. (1996) suggested that haddock on Georges Bank may not comprise a genetically discrete stock. They hypothesized that significant heterogeneity in haplotype frequencies observed in haddock samples from the 1975 and 1985 cohorts from Georges Bank was caused by episodic intrusions of Scotian Shelf surface water onto the bank resulting in larvae from different regions contributing to the gene pool of haddock in this area. However, Purcell et al.

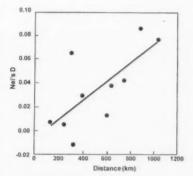


Figure 13.—Relationship between genetic difference (Nei's *D*) and geographic distance separating haddock on northwest Atlantic banks (Zwanenburg et al., 1992).

(1996) also recognized that heterogeneity in mtDNA markers may have been due to mixing of the spawning aggregations on the Northeast Peak and Nantucket Shoals.

Discussion

Current management units for haddock in the northwest Atlantic tend to encompass discrete populations identified on a biological stock basis, although further investigation into the stock structure of haddock in New England and Nova Scotian waters is required (Table 2). Correspondence of the species' biological stock structure with that of its current management units was largely the result of the overriding importance of haddock and Atlantic cod, Gadus morhua, to the fishery when the stock boundaries in the northwest At-

lantic were originally identified in 1932 by the North American Council on Fishery Investigations, and in 1951 by the International Commission for the Northwest Atlantic Fisheries, as information on stock separation was only available for these two species at those times (Halliday and Pinhorn, 1990).

Stock Structure

Throughout the northwest Atlantic, haddock stock structure is divided into three components (New England, Nova Scotia, Newfoundland) by the Fundian and Laurentian Channels that act as barriers to dispersal (Needler, 1930). Within each of these major population divisions, a number of separate haddock stocks exist.

Tag-recapture data, growth rate information, and spawning and circulation patterns within New England waters indicate that there is a resident stock of haddock on Georges Bank (Div. 5Z) and a separate seasonally migrating stock along the coast of the Gulf of Maine (Div. 5Y) (Needler, 1930; Schroeder, 1942; Grosslein, 1962; Smith and Morse, 1985). Growth and spawning data suggest that a discrete stock may also be present in the Nantucket Shoals region (Needler, 1930; Smith and Morse, 1985), although haddock from this area may be a mixture of fish from the Gulf of Maine and Georges Bank. Separation of these stocks may be enhanced by the Great South Channel, although it probably does not have the same effect on dispersal as the other much deeper channels in the northwest Atlantic. A considerable degree of uncertainty still remains in the current views of haddock stock structure within New England waters, particularly over the discreteness of the Nantucket Shoals population and, to a lesser extent, that in the Gulf of Maine.

A range of stock identification techniques suggests a complex stock structure is evident for haddock along the Scotian Shelf, although there is disagreement over the amount of separation (Table 2). At least two major stock divisions occur in Nova Scotian waters, comprising haddock from an eastern (Div. 4TVW) and western Scotian Shelf stock (Div. 4X) (Martin, 1953; Grosslein,

1962: Bowen, 1987). These stocks appear to be relatively distinct with limited mixing between them except along the coast during summer when haddock from inshore waters of the western stock move eastward, and in winter when those from the eastern stock move southwest (McCracken3). However, Frank (1992) found that the spatial dynamics of haddock year classes on the Scotian Shelf are consistent with a pattern of unidirectional mixing of stocks during the pelagic juvenile stage, then a mixed-stock composition up to the age of maturation, followed by a return migration of adult fish to their natal sites. Consequently, Frank (1992) suggested that the management unit on the Scotian Shelf should include both Division 4X and Division 4VW stocks until the potential flux across these stock boundaries is resolved.

Haddock from the eastern Scotian Shelf stock appear to be closely related to those in the southern Gulf of St. Lawrence, and probably belong to the same stock (Halliday, 1971), although comparative data for these regions are limited. Lack of biological data for stock discrimination from the eastern Scotian Shelf and the southern Gulf of St. Lawrence precludes confirmation of these purported stock units. Few haddock have been tagged in these waters to determine movement patterns, and samples required for demographic and spawning patterns have been limited. Uncertainty exists over the stock status of inshore haddock from the southern Scotian Shelf and Bay of Fundy stock (Div. 4X); however, haddock in the latter area may be a mixture from the Gulf of Maine and western Scotian Shelf stocks

Although little tagging data exist for haddock in Newfoundland waters, eastern Scotian Shelf waters, and the southern Gulf of St. Lawrence, it is reasonable to assume that there is little interchange between haddock from these areas and those to the southwest, as the Laurentian Channel is probably an even more effective barrier than the Fundian Channel since it is considerably wider and deeper (Needler, 1930). Within Newfoundland waters, two main haddock stocks exist, one on Grand Bank

(Div. 3LNO) and the other on St. Pierre Bank (Div. 3Ps) (Table 2). Haddock from these two areas are thought to not mix extensively and are considered to be separate stocks based on persistent differences in growth rates and year class compositions (Templeman, 1953; Grosslein, 1962; Templeman and Bishop, 1979a; Halliday and Pinhorn, 1990).

Stock Identification Techniques

Combined information from tag-recapture, demographic, spawning, recruitment, meristic, parasitic, and genetic studies have provided evidence for the identification of haddock stocks throughout the northwest Atlantic (Table 2). Tag-recapture data identified a broad-scale pattern of haddock stock structure in the northwest Atlantic, but provided no conclusive information on stock structure within each of the major regions (Needler, 1930; Schroeder, 1942; McCracken, 1960; Halliday and McCracken, 1970). Recapture data, however, first indicated that New England and Nova Scotian stocks may not be homogeneous units, but instead may be comprised of a number of separate stocks (Needler, 1930; Halliday and McCracken, 1970).

Growth differences between haddock from regions within the northwest Atlantic provided evidence in support of tagging results, which indicated that haddock may return to the same locality to spawn (Needler, 1930; Schuck and Arnold, 1951), resulting in stocks being reproductively isolated and demographic differences subsequently maintained. Zwanenburg et al. (1992) also suggested that haddock home with high fidelity to their natal banks to spawn. thereby maintaining stock separation. Consequently, the amount of mixing between different parts of the population of the different regions may not be sufficient to mask local stock differences (Needler, 1930).

Meristic studies agreed with the general stock structure of haddock proposed by Needler (1930), although they indicated that there may be three to four separate stocks within Nova Scotian waters (Clark and Vladykov, 1960; Tremblay et al., 1984; Vladykov⁷). In

contrast, conflicting genetic results have not improved our understanding of haddock stock structure in the northwest Atlantic, because mtDNA procedures may not be sensitive enough to identify fine-scale population structure (Purcell et al., 1996). The incongruity between the studies of Zwanenburg et al. (1992) and Purcell et al. (1996) is probably partly responsible for the lack of consideration of genetics in the delineation and management of the species stocks. The utility of genetic-based methods in providing a clearer resolution of haddock stock structure will require considerably more samples (Purcell et al., 1996), both of a temporal and spatial component. In addition, a detailed understanding of the extent of both current and historical divergence of haddock stocks will enable assessment of historical changes in stock structure (Purcell et al., 1996).

The various techniques used to identify stock structure of haddock in the northwest Atlantic have tended to agree on the major stock divisions between New England, Nova Scotia, and Newfoundland waters, but they have differed partly in the degree of separation found within each of these regions (Table 2). These differences are probably related to the sensitivity of each method in detecting stock separation and the limitations associated with each technique. Tagging studies of haddock have generally been restricted to inshore waters in spring and summer, with few fish having been tagged on important offshore banks where major spawning aggregations occur (Needler, 1930; Schroeder, 1942; McCracken, 1960; Halliday and McCracken, 1970). Consequently, the degree of interchange between stocks from inshore and offshore fishing grounds and their relative discreteness cannot be determined from these studies. Typically, the demographic studies have only presented average length-at-age data, thereby precluding examination of the amount of variability in the data and the level of significance used to determine differences in stock dynamics (Needler, 1930). Gear selectivity problems, differences in sampling times, and the general lack of homogeneity in samples have also tended to confound the results of these studies (Schuck and Arnold, 1951; Hennemuth et al., 1964).

Spawning (Grosslein and Hennemuth, 1973; Sherman et al., 1984; Smith and Morse, 1985; Lough and Bolz, 1989), recruitment (Clark et al., 1982; Koslow, 1984; Koslow et al., 1987; Thompson and Page, 1989), meristic (Clark and Vladykov, 1960; Tremblay et al., 1984; Vladykov⁷), parasitic (Scott, 1981), and genetic (Zwanenburg et al., 1992; Purcell et al., 1996) stock identification studies of haddock have usually been restricted in their temporal and spatial comparisons, effectively preventing examination of the temporal persistency in stock structure patterns. Inadequate spatial samples, particularly from inshore waters, have made it difficult to determine the connectivity and relative separation of stocks found on inshore and offshore fishing grounds, a topic that requires considerably more investigation if a finer resolution of haddock stock structure in the northwest Atlantic is to be achieved.

Future Research

Stock identification is a necessary precursor for effective fisheries management (Kutkuhn, 1981). Although a number of haddock stocks in the northwest Atlantic have been identified using a combination of traditional techniques, uncertainty remains in the discreteness of stocks in New England and Canadian waters. This lack of understanding of haddock stock structure can limit the ability to develop and implement effective stock rebuilding programs throughout the region. Such knowledge is useful for setting management restrictions in fisheries which contain several stocks with different levels of exploitation, as less productive stocks may be seriously depleted or eliminated if exploited with fishing rates that adequately exploit more productive stocks in a mixed fishery (Ricker, 1958).

Future research examining the stock structure of haddock in these regions should advance existing studies by utilizing more recent, innovative stock identification techniques such as chemical analysis of calcified structures that have proved useful for differentiating among Atlantic cod stocks (Campana et al., 1994). Contemporary stock identification tools such as otolith marking and image analysis procedures should also be investigated to determine their utility for discrimination of haddock stocks in the northwest Atlantic. A combination of techniques should be used in unison to strengthen and confirm any suggested stock structure provided by a single procedure in isolation owing to the inadequacies associated with any particular method (i.e. an integrated holistic approach to stock identification) (Begg and Waldman9).

Population dynamic models used in fisheries management need to be developed that incorporate multistock complexes and demographic consequences of dispersal, such as the more recent metapopulation models (Frank, 1992). Such models may be particularly relevant for haddock stocks along the Scotian Shelf and in other regions of the northwest Atlantic that appear to migrate and mix with other stocks at certain times of the year. Although most fisheries are managed on a single-species basis, there is a general recognition that multispecies interactions are an important component of marine ecosystem dynamics which should be considered in contemporary management plans (Mahon and Smith, 1989). Likewise, multistock models, as is evident for haddock in the northwest Atlantic, should be developed and applied in a similar context to multispecies models. Conceptually, species and stocks can be viewed as the same unit or level of hierarchy in these models, although by definition of a species, more gene flow would be expected between stocks of the same species than between species, but treatment of the two units could be the same.

Stock structure information provides a basis for understanding the dynamics of fish populations that assists scientists and managers in predicting how a stock may respond to different management strategies. Investigation into the tempo-

⁹ Begg, G. A., and J. R. Waldman. An holistic approach to fish stock identification. Manuscr. in review.

ral stability and historical shifts in stock structure of haddock throughout the northwest Atlantic via archived biological samples and data sets in relation to environmental fluctuations and effects of the fisheries, will enable an historical perspective of stock structure to be developed. This would assist in understanding the collapse of haddock stocks throughout their distribution and the implications of these effects to current stock assessment, rebuilding, and management plans. Consequently, identification of haddock stocks and their rates of mixing should continue to undergo investigation in order to refine our understanding of haddock stock structure in the northwest Atlantic.

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Biological Characteristics and Fishery Assessment of Alaska Plaice, *Pleuronectes quadrituberculatus*, in the Eastern Bering Sea

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Introduction

The Alaska plaice, *Pleuronectes* quadrituberculatus (Fig. 1), is a right-eyed flounder, family Pleuronectidae, and one of four shallow-water flatfishes, along with the yellowfin sole, *Pleuronectes* asper; rock sole, *Pleuronectes* bilineatus; and flathead sole, *Hippoglossoides* elassodon, commonly found in the eastern Bering Sea. They inhabit continental shelf waters of the North Pacific Ocean ranging from the Gulf of

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Alaska to the Bering and Chukchi Seas and in Asian waters as far south as the Sea of Japan (Fig. 2) (Pertseva-Ostroumova, 1961; Quast and Hall, 1972).

The Alaska plaice is a relatively large flounder, with an average length taken in commercial catches of 32 cm (12.6 inches) while the average weight caught is 390 g (0.86 lb.). This corresponds to an age of 7 or 8 years. Moiseev (1953) reported a maximum length of 60 cm (23.6 inches), and ages in excess of 30 years have been determined for fish collected from NMFS Alaska Fisheries Science Center (AFSC) surveys (data on file, AFSC).

In this paper, we examine available information on Alaska plaice to provide

1) a detailed description of the life history characteristics of eastern Bering Sea Alaska plaice, including growth and mortality, age at maturation and spawning, and feeding habits and ecological interactions; 2) the history of its exploitation and trends in estimated abundance; 3) the current condition of the resource and 4) projections of future biomass under various harvest levels.

Materials and Methods

Information Sources

Information for this paper came from both a review of the available literature on the biology of Alaska plaice and from analyses of research and fishing data. Information from the literature was primarily used to describe the distribution and such life history parameters as age and growth, age at maturation and spawning, fecundity, feeding habits, and ecological interactions with other species. Data from AFSC trawl surveys and the fishery were analyzed to describe size composition, size and age at maturity, fecundity at length relationships, abundance and biomass by year and age, and annual recruitment.

Assessment Methods

Resource Assessment Surveys

Since 1971, the AFSC has conducted summer bottom-trawl surveys in the eastern Bering Sea to estimate abundance and study the biology of important fish and invertebrate species. In 1975, and annually since 1979, these surveys have covered the major portion

ABSTRACT—Alaska plaice, Pleuronectes quadrituberculatus, is one of the major flatfishes in the eastern Bering Sea ecosystem and is most highly concentrated in the shallow continental shelf of the eastern Bering Sea. Annual commercial catches have ranged from less than 1,000 metric tons (t) in 1963 to 62,000 t in 1988. Alaska plaice is a relatively large flatfish averaging about 32 cm in length and 390 g in weight in commercial catches. They are distributed from nearshore waters to a depth of about 100 m in the eastern Bering Sea during summer, but move to deeper continental shelf waters in winter to escape sea ice and cold water temperatures. Being a long-lived species (>30 years), they have a relatively low natural mortality rate estimated at 0.20.

Maturing at about age 7, Alaska plaice spawn from April through June on hard sandy substrates of the shelf region, primarily around the 100 m isobath. Prey items primarily include polychaetes and other marine worms. In comparison with other

flatfish, Alaska plaice and rock sole, Pleuronectes bilineatus, have similar diets but different habitat preferences with separate areas of peak population density which may minimize interspecific competition. Yellowfin sole, Pleuronectes asper, while sharing similar habitat, differs from these two species because of the variety of prey items in its diet. Competition for food resources among the three species appears to be low.

The resource has experienced light exploitation since 1963 and is currently in good condition. Based on the results of demersal trawl surveys and age-structured analyses, the exploitable biomass increased from 1971 through the mid-1980's before decreasing to the 1997 level of 500,000 t. The recommended 1998 harvest level. Allowable Biological Catch, was calculated from the Baranov catch equation based on the F_{MSY} harvest level and the projected 1997 biomass, resulting in a commercial harvest of 69,000 t, or about 16% of the estimated exploitable biomass.

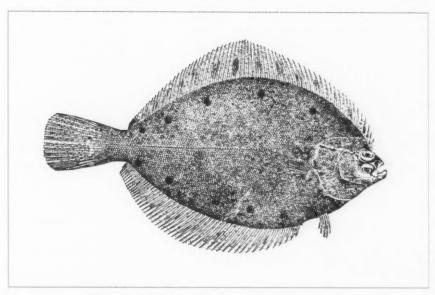


Figure 1.—The Alaska plaice, Pleuronectes quadrituberculatus.

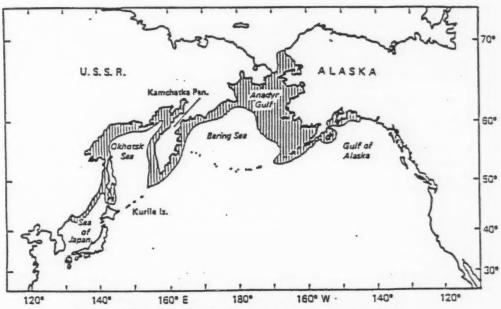


Figure 2.—Overall distribution of Alaska plaice, Pleuronectes quadrituberculatus.

of the continental shelf to lat. 61°N (465,000 km²). The depth range covered by the standard survey extends from about 10 m near the mainland to about

200 m at the shelf break (subareas 1–6 in Fig. 3). Although the survey's primary role is to provide fishery-independent abundance estimates for manage-

ment purposes, they also provide a wealth of biological information on the multispecies complex of fishes that inhabits the eastern Bering Sea.

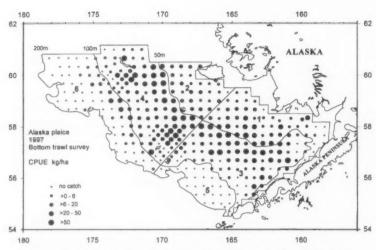


Figure 3.—Summer distribution and relative abundance in kg/ha of Alaska plaice from the 1997 eastern Bering Sea bottom trawl survey. Depth contours and statistical subareas are indicated.

The standard survey area on the shelf is divided into a grid with 37 × 37 km blocks (20 × 20 n.mi.) containing a sampling location at the center of each grid block. In areas of special interest, the corners of the blocks have also been sampled. The sampling gear is a standard AFSC eastern otter trawl with a 25.3 m headrope and 34.1 m footrope. Otter doors are 1.8×2.7 m and weigh about 800 kg each. At each sampling site the trawl is towed for 0.5 h at a speed of 5.6 km/h. The operating width between the wings varied from about 10 to 18 m as a function of the amount of trawl warp payed out and therefore indirectly as a function of depth. The operating trawl height varied from 2 to 3 m as determined from net mensuration. Due to the relatively flat, unobstructed bottom on the shelf, the trawl is operated without roller gear. To improve the catches of invertebrates, the trawl was rigged to dig slightly into the bottom.

Estimates of biomass and population are made using the "area swept" method described by Wakabayashi et al. (1985). The mean catch per unit of effort (CPUE) of a group of tows of known area swept is expanded to estimate the biomass within the total area of a stratum (Armistead and Nichol, 1993). The area swept is considered to be the product of the operating net width between

the wings and the distance fished. The potential herding effect of the doors and dandylines is unknown for Alaska plaice, as is escapement under the footrope.

Age-structured Analyses

Biomass-based cohort analysis, after Zhang and Sullivan (1988), were applied to Alaska plaice catch at age data from 1971 to 1995 by Wilderbuer and Zhang (In press). This method assumes knife-edge recruitment with equal availability for all recruited ages and constant natural mortality over all ages and years. The input terminal fishing mortality values were estimated using the following formula:

$$F_{95} = \frac{C_{95}}{B_{95}}$$

where B_{95} is the 1995 trawl survey biomass estimate, and C_{95} is the 1995 catch in weight. The second run of the analysis was conducted using the tuned terminal fishing mortality values, which were tuned to different ratios of mean fishing mortalities by age and by year.

Wilderbuer and Zhang (In press) also incorporated age composition information from a variety of sources into a stock synthesis model (Methot, 1990) for Alaska plaice. Stock synthesis functions by simulating the dynamics of the

population and the process by which the population is observed. The simulation incorporates bias and imprecision in the observations and is used to predict expected values for the observations. The expected values are compared to the actual observations (data) from the surveys and fisheries.

The biomass-based approach to the production model (Zhang, 1987; Zhang et al., 1991) was also utilized to analyze biomass and fishing mortality and to provide estimates of the important management parameters MSY, B_{MSY} and F_{MSY} . The model was used to project the future biomass of the Alaska plaice stock and catch under various F levels, including the current F level.

Optimal Fishing Mortality and Age at First Capture

Yield per recruit analysis was performed using the Beverton and Holt (1957) model to estimate the optimal fishing mortality and age at first capture. Age at first capture (t_c) was varied from 1.0 to 10.0 and the annual instantaneous rate of fishing mortality was varied from 0.01 to 0.30.

History of Exploitation

Groundfish species in the eastern Bering Sea were first exploited commercially by Japan, initially by exploratory vessels in 1930 and then by a mothership-catcher boat operation in Bristol Bay in 1933-37 and 1940-41 (Forrester et al., 1978). From 1933 to 1937, walleye pollock, Theragara chalcogramma, and various flounders (family Pleuronectidae) were reduced to fish meal, and annual Japanese catches peaked at 43,000 metric tons (t). During 1940-41, the fishery targeted on yellowfin sole, Pleuronectes asper, for human consumption, and catches ranged from 9,600 to 12,000 t (Forrester et al., 1978).

After World War II, Japanese distantwater fleets resumed operations in the eastern Bering Sea, with motherships and independent trawlers targeting yellowfin sole in 1954. In 1958 the U.S.S.R. also entered the fishery, followed by other nations in later years.

Catch statistics for Alaska plaice cannot be precise for the earlier years because the species was often included in the "other flatfish" category. Catch composition data improved in later years, particularly after implementation of the Magnuson Fishery Conservation and Management Act of 1976 (MFCMA) which established the foreign fishery observer program. The Alaska plaice catch (Table 1) was low until the resumption of the U.S.S.R. fishery in 1978 and

onset of the harvests by the Republic of

Korea and other nations in 1980. Alaska plaice share similar habitats and distributions with yellowfin sole and are taken as bycatch with that species. Yellowfin sole were intensely harvested by distant-water fleets from Japan and the U.S.S.R. in the early 1960's with a peak catch of 554,000 t in 1961. High exploitation during the 4-year period from 1959 to 1962 caused the population to decline which was reflected in the reduced harvest over the following two decades (Wilderbuer et al., 1992). From 1963 to 1971, however, vellowfin sole annual catches still averaged 117,800 t. Given the similarity of the distributions, the yellowfin sole fishery probably removed a significant portion of the Alaska plaice population through bycatch. Catches for the period 1963–71 in Table 1, therefore, are likely underestimated.

After the cessation of foreign fishing in 1987, the Alaska plaice harvest peaked at over 61,000 t during U.S. joint-venture fisheries in 1988. Catches therafter have been made by the U.S. domestic fishery, with an annual average of 14,800 t. Based on results of cohort analysis and stock synthesis analysis, the stock has been lightly harvested, with an average exploitation rate of less than 5% since 1971 (Wilderbuer and Zhang, In press).

Biological Characteristics

Distribution and Migration

The summer distribution of Alaska plaice in the eastern Bering Sea is almost entirely restricted to depths of less than 110 m, with major concentrations between 40 and 100 m on the central and northern Bering Sea shelf (Fig. 3). Fish >25 cm predominate in the sampled population between 20 and 110 m. Larger fish generally prefer such deeper

Table 1.—Annual catches of Alaska plaice in metric tons (t) by fishing nation in the eastern Bering Sea, 1963-97.

	Catch (t)							
Year	Japan	U.S.S.R.	ROK	Other	Joint Venture	Domestic U.S.	Total	
1963	233	746	0	0	0	0	979	
1964	808	1,085	0	0	0	0	1,893	
1965	484	516	0	0	0	0	1.000	
1966	2.054	2,579	0	0	0	0	4,633	
1967	1,339	2,513	0	0	0	0	3,852	
1968	1.233	1,396	0	0	0	0	2,629	
1969	3,127	3,815	0	0	0	0	6.942	
1970	1,356	2,125	0	0	0	0	3,481	
1971	533	490	0	0	0	0	1,023	
1972	191	139	0	0	0	0	330	
1973	1,136	40	0	0	0	0	1,176	
1974	2,168	220	0	0	0	0	2,388	
1975	2,408	84	0	0	0	0	2.492	
1976	3,518	102	0	0	0	0	3,620	
1977	2.589	0	0	0	0	0	2,589	
1978	5.204	5,216	0	0	0	0	10.420	
1979	3.767	9.896	9	0	0	0	13.672	
1980	3,810	0	2,978	120	0	0	6,908	
1981	7,298	0	1,315	40	0	0	8.653	
1982	5,451	0	1,144	216	0	0	6,811	
1983	5,790	0	3,126	1,850	0	0	10,766	
1984	10,405	1,573	4.012	2,992	0	0	18.982	
1985	5.702	265	4,833	14,088	0	0	24,888	
19861			46.519		0	0	46,519	
19871			18,567		- 0	0	18.567	
1988	0	0	0	0	61,638	0	61,638	
1989	0	0	0	0	13.883	0	13.883	
1990	0	0	0	0	6.080	0	6,080	
1991	0	0	0	0	0	18.029	18,029	
1992	0	0	0	0	0	18,895	18,895	
1993	0	0	0	0	0	14,536	14,536	
1994	0	0	0	0	0	9,277	9.277	
1995	0	0	0	0	0	13.343	13.343	
1996	0	0	0	0	0	16,106	16,106	
1997	0	0	0	0	0	19,829	19,829	

Catch of Alaska plaice by nation is presently unavailable.

waters (Bakkala et al., 1985), while juveniles (< 20 cm) occupy shallower coastal waters (Wakabayashi, 1972). This difference in depth preference provides a buffer between the juvenile and adult populations. Annual AFSC trawl surveys also indicate a summertime sexual segregation: female catch rates are greatest at depths > 60 m, while the highest catch rates for males occur at 45–55 m depths.

Fadeev (1965) suggests that Alaska plaice live year round on the shelf and move seasonally within its limits. Water temperatures may influence the seasonal movements and subsequent distribution on the shelf. Alaska plaice maintain a more westerly wintertime distribution (Fig. 4), possibly to avoid the cold bottom water temperatures that exist over the eastern Bering Sea shelf during winter. However, the extent of ice coverage may be limiting the distribution of fishing effort which is used to discern the wintertime distribution; restricting our knowledge of their seasonal distribution.

Alaska plaice are rarely encountered on the slope during the winter. They may reach the outer shelf in winter together with yellowfin sole, as was observed during spring 1976, but they generally prefer shallow water. Although this species distribution overlaps with rock sole, *Pleuronectes bilineata*, and yellowfin sole, the center of abundance of Alaska plaice is located to the north of the other species.

Early Life History

The eggs and larvae of Alaska plaice are pelagic and transparent, with egg diameter ranging from 1.9 to 2.05 mm (Musienko, 1963; Waldron, 1981; Matarese et al., 1989). Pertseva-Ostroumova (1961) described the embryonic and larval development of Alaska plaice from the west coast of Kamchatka and reported that artificially fertilized eggs, incubated at an average temperature of 6°C, hatched in 15.5–18 days. Eggs developing under natural conditions (-1.5°-6.7°C) may have a longer incubation period.

Little is known about the distribution of Alaska plaice eggs. The available data suggests the eggs are widely distributed

Table 2.—Summary of Alaska plaice egg distribution information from results of ichthyoplankton surveys conducted in the eastern Bering Sea.

Authority	Time period	Method	Findings
Waldron and Favorite (1977)	April-May 1976	Bongo and neuston nets	Eggs widely distributed with centers of abundance near the outer Alaska Peninsula, east of the Pribilof Islands, outer Bristol Bay and northwest of the Pribilof Islands
Waldron and Vinter ¹ (1978)	May 1977	Bongo and neuston nets	Eggs comprised 28% of bongo samples and 72% of the neuston net samples at 64 locations. Eggs had a wide distribution over the Bering Sea shelf.
Waldron (1981)	1955–79	Bongo and neuston nets	Eggs were widely distributed from lat. 55°N off Unimak Island to lat. 59.5°N near Nunivak Island and from long. 159°W in Bristol Bay to long. 175°W near the shelf edge.

¹ Waldron, K. D., and B. M. Vinter. 1978. Ichthyoplankton of the eastern Bering Sea. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Seattle, Wash., NWFC Processed Rep., 88 p.

over the continental shelf of the Bering Sea and have been found in varying densities and spatial concentrations among the years sampled (Table 2). Spawning is believed to occur during March-April, and eggs are found from April to early summer.

Upon hatching, Alaska plaice larvae are apparently more developed than other flounders. The larvae are relatively large at hatching (5.85 mm) and have advanced body differentiation and eye pigmentation, which may be an adaptation to development at high latitudes and low temperatures (Pertseva-Ostroumova, 1961). Small larvae are mainly found in the surface layer, although they occasionally are caught as deep as 120 m. The volk sac, ranging from 0.68 to 1.5 mm long and 0.32 to 0.60 mm high, is absorbed when the larvae are about 6.0-7.5 mm in length. Although the length at which metamorphosis occurs is unknown, young larvae of Alaska plaice appear to become demersal at a length of about 13-17 mm (Pertseva-Ostroumova 1961).

Growth and Mortality

Alaska plaice is a slow-growing longlived species, typical of eastern Bering Sea shelf flatfish. Age and growth studies have been conducted by Mosher (1954), Weber and Shippen (1975), Bakkala et al. (1985), and Zhang (1987), based on an examination of otoliths. Male and female fish have been aged up to 31 years, and ages greater than 25 are not uncommon for fish in trawl survey catches. Length-at-age is similar for males and females until about ages 8-10 (30-32 cm) when male growth slows with the onset of sexual maturity (Fig. 5). It is not known whether differential growth by geographic region occurs on the eastern

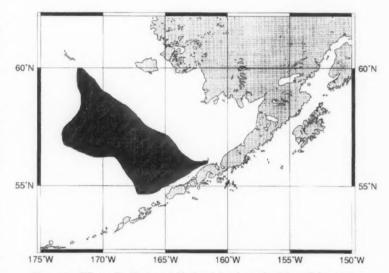


Figure 4.—Winter distribution of Alaska plaice determined from fishery sampling, 1978–96.

Bering Sea shelf. Parameters for the von Bertalanffy equation from age structures collected in 1988 are as follows:

	L_{∞} (mm)	t_0	K
Males	379.2	1.83	0.204
Females	501.7	2.09	0.156

Values of *K* are low for both sexes, indicative of slow growth. It is expected that the natural mortality rate (*M*) of such a slow-growing, long-lived species would also be relatively low. Estimates of *M* range from 0.195 to 0.22 for Alaska place (Wilderbuer and Zhang, In press). Natural mortality is likely close to 0.2, which is the value used in age-structured modeling of the eastern Bering Sea population (Wilderbuer and Walters, 1997).

The length-weight relationships for males and females from the 1990 survey are shown in Figure 6. The param-

eters for the relationship, weight in grams = $a(\text{length in cm})^b$ are:

	a	b
Males	.05677	2.576
Females	.006148	3.217

Although the length-weight relationships for males and females are similar, Zhang (1987), using data collected during the 1975 AFSC survey, reported that large females (> 26 cm) were up to 7% heavier than males of the same size.

Maturation and Spawning

During 1986–87, female Alaska plaice taken by the commercial fishery were classified as to maturity state by U.S. observers using the criteria presented in Table 3. Most of the females examined were in the developing stage (Code 2) in March, in the spawning stage (Code 3) in

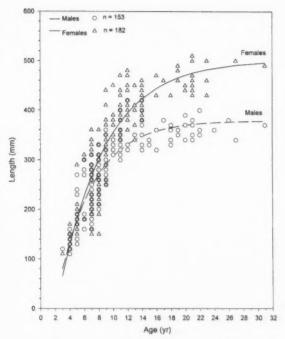
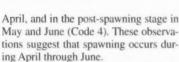


Figure 5.—Age-length distribution of Alaska plaice as determined by samples collected during the 1988 eastern Bering Sea bottom trawl survey. Curves are from nonlinear regression of the von Bertalanffy equation.



The length at maturity for female Alaska plaice was also determined from a sample of fish examined during March and April by fitting a logistic equation to the relationship between length and the proportion of mature females (Fig. 7), as follows:

$$P_{L} = \frac{1}{1 + \exp{\frac{(-(L - L_{0.50}))}{C}}},$$

where L = length in centimeters, P_L = proportion mature at length L, $L_{0.50}$ = length where: P_L =0.50 = maturation length and c is a constant. The above equation can be linearized to: $ln(1/P_L - L)$ = $L_{0.50}/c - 1/c$.

The equation is then of the form Y = a + bX, and a weighted linear regression of $\ln(1/P_L - L)$ on L can be applied. The weights used for Y observations

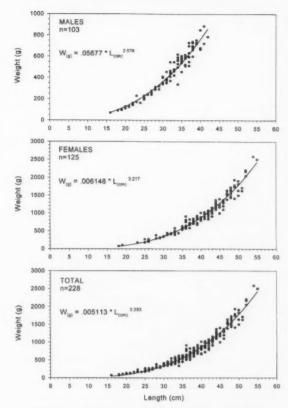


Figure 6.—Length versus weight relationships for Alaska plaice sampled during the 1990 eastern Bering Sea bottom trawl survey. Lines and equations are the result of nonlinear regression of the function, weight_(g)=a (length_(cm)^b).

Table 3.—Criteria used to classify Alaska plaice by maturity stage.

Maturity		
Code	Stage	Description of gonads
1	Immature	Gonad small, situated close to vertebral column. Difficult to determine sex. Ovaries orangish to translucent, testes translucent. Apparently has not spawned for the first time.
2	Developing	Gonad small, to about $^{1/2}$ length of ventral cavity. Transparent and/or opaque ova visible to naked eye, testes more opaque and swelling.
3	Spawning	Ova and sperm run under slight pressure. Most eggs translucent with few opaque eggs left in pale orange ovary.
4	Spent	Ovaries and testes flaccid and empty. Ovaries may contain remnants of disintegrating ova, testes bloodshot.
5	Inactive	Adults with gonads firm and shaped, but showing no development of ova or sperm.

were $1/\text{Var}(Y) = nP_L \ (1-P_L)$ (Gunderson, 1977). Regression coefficients obtained were then used to estimate $L_{0.50} = (-a/b)$ and c = (-1/b).

The variance of $L_{0.50}$ was approximated by using the delta method:

$$Var(L_{0.50}) = \frac{1}{b^2} Var(a) + \left(\frac{a}{b^2}\right)^2 - 2\left(\frac{1}{b^3}\right) Cov(a,b)$$

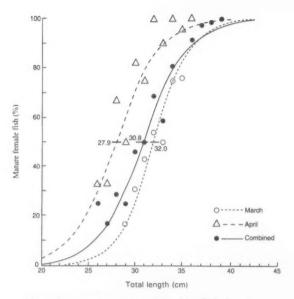


Figure 7.—Length-maturity relationship of Alaska plaice in the eastern Bering Sea, based on data collected by U.S. observers from the fishery.

The parameter estimates for the proportion mature at length, predicted length at 50% maturity L(0.50) and standard errors for $L_{0.50}$ are presented in Table 4. The estimated $L_{0.50}$ was 32 cm from collections made in March and 28 cm from April. The combined value was 31 cm, which corresponds to an age of 6 to 7 years. Pertseva-Ostroumova (1961) reports that Alaska plaice from Asian waters reach sexual maturity at 4-6 years corresponding to a length of 20-21 cm. This may indicate a smaller size at maturity in Asian waters than in the eastern Bering Sea. However, it is difficult to suggest the existence of differences in age at maturity by area, since there is a large temporal difference in the collection times of the two samples.

Fecundity estimates (Fadeev, 1965) from the southeastern Bering Sea indicate female fish produce an average of 56,000 eggs at lengths of 28–30 cm, and 313,000 eggs at lengths of 48–50 cm (Table 5). Fertilization is external. Spawning of Alaska plaice is reported to occur over a 2–3 month period during the spring on hard sandy substrates of the shelf region, primarily around the 100 m isobath within a range of 75–150

m (Pertseva-Ostroumova, 1961). The annual spawning period may vary both temporally and spatially due to the variations in hydrological conditions. In the Bering Sea, Musienko (1970) reported that spawning apparently starts in early spring immediately after the ice melts (early May) and continues until mid-June. He also found that peak spawning in this region occurs at water temperatures ranging from -1.53° to 4.11°C and salinities ranging from 29.8% to 34% on the seafloor and 32% to 32.8% at the surface. Alaska Fisheries Science Center observations on the duration and timing of spawning generally agree with those of Pertseva-Ostroumova (1961) and Musienko (1970), although the AFSC data suggest that peak spawning may occur in April.

Observations from egg and larval surveys, however, indicate spawning may occur as late as June (Waldron and Vinter¹). This variation in the time of spawning may result from variations in

Table 4.—Estimates of parameters for the logistic equation of the relationship between length and the proportion of mature female Alaska plaice in the eastern Bering Sea. Predicted length at maturity (L_{0.50}) and the standard error for f_{0.50} are also shown.

Sample month	Proportion mature	L _{0.50} (cm)	S.E. L _{0.50} (cm)
March	0.5379	31.9985	0.2827
April	0.4418	27.9005	7.3571
Combined	0.4300	30.8013	0.3012

Table 5.—Fecundity of Alaska plaice in the southeastern Bering Sea from a sample of 47 fish (Fadeev, 1965).

Length (cm)	Fecundity (x 1,000)
28.1-30.0	56.3
30.1-32.0	93.2
34.1-36.0	127.2
36.1-38.0	159.5
38.1-40.0	161.8
40.1-42.0	183.0
42.1-44.0	268.5
44.1-46.0	280.8
46.1-48.0	289.3
48.1-50.0	312.6

hydrographic conditions as suggested by Pertseva-Ostroumova (1961).

Alaska plaice do not aggregate for spawning but spawn over a wide area of the middle shelf. Northeasterly surface currents move the eggs to shallower waters of Bristol Bay and other coastal areas of the Alaska mainland where young plaice apparently live until they grow to about 20 cm in length. Eggs may also drift from the eastern Bering Sea to the Chukchi Sea through the Bering Strait. A strong current runs northward from the Bering Sea through the Bering Strait and into the southeastern Chukchi Sea (Pruter and Alverson, 1962). Current speeds of 0.25-0.50 m/sec have been reported from the surface to within a few meters of the bottom in the eastern Chukchi Sea and along the Alaska coast during summer (Fleming et al.2). Alaska plaice length frequency distributions collected from the Chukchi Sea in 1977, were comprised mostly of juveniles ranging from 10 to 20 cm in length although some were as large as 40 cm (12 years) (Wolotira et al.³).

Waldron, K. D., and B. M. Vinter. 1978. Ichthyoplankton of the eastern Bering Sea. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Seattle, Wash., NWAFC Processed Rep. (unnumbered: Final Rep. (RU 380)), 88 p.

² Fleming, R. H. 1959. Oceanographic survey of the Chukchi Sea 1 August to 2 September 1959. Preliminary report of Brown Bear cruise No. 268. Univ. Wash., Dep. Oceanogr., Seattle, Mimeogr. Rep. 59-30:1-14.

³ Wolotira, R. J., Jr., T. M. Sample, and M. Morin, Jr. 1977. Demersal fish and shellfish resources of Norton Sound, the southeastern Chukchi Sea, and adjacent waters in the baseline year 1976. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., NWAFC Processed Rep. (unnumbered), 292 p.

Table 6.—Prev diets of Alaska plaice in the Bering Sea.

Authority	Bering Sea area	Major food items
Skalkin (1963)	Southeastern	Benthic crustaceans, mollusks, polychaetes
Mineva (1964)	Eastern	Bivalves, gastropods, polychaetes
Feder (1977, 1978)	Eastern	Polychaetes, bivalves, amphipods, nemerteans
Allen1 (1984)	Southeastern	Benthopelagic, epifaunal, sessil infaunal preys
Zhang (1987)	Eastern	Polychaetes, amphipods, Echiura, Sipuncula
Lang (1992)	Eastern	Polychaetes, amphipods, bivalves, decapods

Text footnote 4

Feeding and Ecological Interactions

Food habits of Alaska plaice in the eastern Bering Sea have been studied by Moiseev (1953), Skalkin (1963), Mineva (1964), Feder (1977, 1978), Zhang (1987, 1988), Lang (1992), Lang et al. (1995), and Allen (1984^{4.5}), Skalkin (1963), Zhang (1987, 1988), Lang (1992), Lang et al. (1995), and Allen⁴ also studied trophic interactions among Alaska plaice, yellowfin sole, and rock sole which share a similar habitat and have overlapping distributions.

According to Zhang (1987), the stomach fullness of Alaska plaice was lowest after midnight (0300 to 0600 h), suggesting that feeding does not occur at night. Stomach fullness was greatest in the afternoon (1500 to 1800 h) indicating that feeding seems to be active during daytime, primarily on polychaetes and amphipods regardless of sex and size.

Table 6 shows prey items of Alaska plaice in the Bering Sea. Skalkin (1963) found that the major food items of Alaska plaice in the southeastern Bering Sea were benthic crustaceans, mollusks, and polychaetes. All three major food types were not found to occur in stomach contents at the same time. Rather, the diet often consisted of polychaetes and mollusks or only one of the three groups.

Mineva (1964) examined 190 stomachs of Alaska plaice in the eastern

Bering Sea and found the following important prey items: bivalves such as Yoldia hyperborea, Y. johanni, and Macoma calcarea; gastropods such as Cylichna alba; polychaetes such as Sternaspia scutata, and Scalibregma sp.; Nephtydae; Terebellidae; amphipods; and ophiuroids. Other Bering Sea studies (Feder, 1977, 1978) also found polychaetes, bivalves, amphipods, and nemerteans to be major food items for Alaska plaice. Allen4 examined the stomach contents of Alaska plaice on the southeastern Bering Sea shelf in 1982, and found benthopelagic, epifaunal, and sessil infaunal prey in the stomachs.

Lang (1992) intensively studied the food habits of Alaska plaice from a sample of 513 stomachs, 64 of which were empty and 449 contained food. He found that polychaeta prey was the most commonly occurring prey group, however, gammarid amphipods were also quite common. The other prey items were bivalves, marine worms, decapods and echinoderms (Table 7).

Zhang (1987) found that the pattern of food consumption by size group was very similar, with the most important prey being polychaetes (75.2% for fish >30 cm and 63.3% for fish <30 cm). The next most important items were amphipods (6.7%) and Echiura (5.7%) for the >30 cm group, and Sipuncula (21.7%) and amphipods (11.6%) for the <30 cm group. Fish were only found in the stomachs of the >30 cm group, usually in small amounts.

To examine diet overlap among Alaska plaice, yellowfin sole, and rock sole, Zhang (1987) used Schoener's (1970) index of dietary overlap to compare the similarity of their diets for two taxonomic levels of prey (the lowest taxonomic level and the phylum level, Table 8). The analysis indicated that diet overlap between the three species was

Table 7.—Polled prey diet and Index of Relative Importance (IRI) of Alaska plaice in the eastern Bering Sea (Lang 1992).

Prey taxa	Frequency of occurrence (%)	Numbers (%)	Weight (%)	IRI
Polychaeta	90.4	25.6	60.9	78.2
Bivalvia	37.0	5.5	5.8	4.2
Amphipoda (Gammarida)	70.2	50.0	3.1	37.2
Decapoda	4.7	0.3	0.2	0.02
Marine worms	47.7	11.3	29.0	19.2
Echinodermata	12.7	1.0	0.2	0.2
Fish	1.1	0.05	0.1	0.002
Miscellaneous	25.4	6.3	0.7	1.8

Table 8.—Results of Schoener's index of diet overlap (Schoener, 1970) between Alaska plaice, yellowfin sole, and rock sole of the eastern Bering Sea. Values were calculated for the lowest possible prey taxonomic level and at the phylum level.

Species	Yellowfin sole	Rock sole
Lowest taxonomic level Alaska plaice Yellowfin sole	0.127	0.299 0.154
Phylum level Alaska plaice Yellowfin sole	0.313	0.787 0.517

less than 0.3 for the lowest taxonomic level but as high as 0.8 at the phylum level. The highest values were obtained in comparisons between Alaska plaice and rock sole (C(x,y) = 0.299) at the lowest possible taxonomic level but was relatively high (C(x,y) = 0.787) at the phylum level). The most important common prey of the two species was polychaetes but the prey species of secondary importance differed: Echiura for Alaska plaice and amphipods, Echiura and Echinodermata for rock sole. The diet of yellowfin sole was different from these two species with amphipods and Echinodermata as the most important prev item. Overall, there was less overlap in the diet between Alaska plaice and yellowfin sole than between rock sole and yellowfin sole.

Skalkin (1963) stated that the degree of food similarity between Alaska plaice and yellowfin sole caught in the same trawl was more than 50%. He also found an unusually high degree of food similarity between Alaska plaice and rock sole due to the consumption of polychaetes. Allen⁵ hypothesized that, on the ecological segregation among species of fish, competitive species have the same spatial distribution (habitat)

⁴ Allen, M. J. 1984. Functional organization of demersal fish communities of the eastern Bering Sea. Unpubl. manuscr. on file at U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Northwest Alaska Fish. Cent., 7600 Sand Point Way, N.E. Seattle, WA 98115.

⁵ Allen, M. J. 1984. Niche segregation of nearshore soft-bottom fishes in a subarctic, warm-temperature, and tropical environment. Unpubl. manuscr. On file at U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Northwest Alaska Fish. Cent., 7600 Sand Point Way, N.E. Seattle, WA 98115.

and foraging behavior (niche), while noncompetitive species have either different feeding behavior or spatial distribution. Evidence presented for the three flatfish species considered here would tend to support the hypothesis that these species are not competitive. Schoener's index of diet overlap was highest between Alaska plaice and rock

sole which have the most dissimilar distribution and lowest for Alaska plaice and yellowfin sole which have similar distributions.

Lang et al. (1995) also examined food habits of the three congeneric flatfishes in the eastern Bering Sea and determined that Alaska plaice exhibited the narrowest diet selection, consisting primarily of polychaetes and other worms. This supports Zhang's hypothesis (Zhang, 1987) that the diets of Alaska plaice and rock sole are similar due to their reliance upon polychaetes, while yellowfin sole differed from the two species due to the variety of prey items, and their areas of highest abundance are spatially separate (Fig. 8). Thus, com-

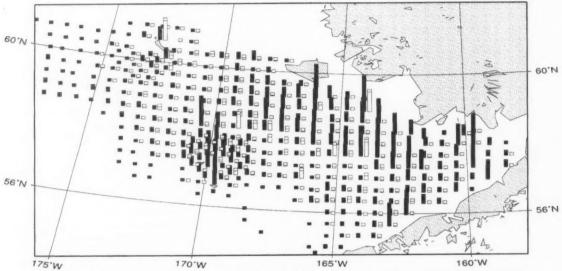


Figure 8a.—Comparison of the distribution and abundance for Alaska plaice (white) and rock sole (dark) from the 1996 trawl survey.

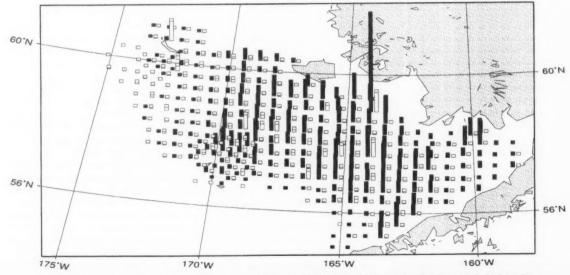


Figure 8b.—Comparison of the distribution and abundance for Alaska plaice (white) and yellowfin sole (dark) from the 1996 trawl survey.

petition for similar prey items among species appeared low. In conclusion, food competition seems to be negligible among the shallow-water flatfish species inhabiting the eastern Bering Sea due to differences in food spectra or spatial distribution. We hypothesize that the abundance and distribution of Alaska plaice may be less than that of yellowfin sole, because Alaska plaice are more specialized in terms of their food habits.

Fluctuations in Abundance

Annual Changes in Population Biomass

The annual estimates of biomass from two age-structured models (Fig. 9) indicate a continuous increase in abundance from 1971 through the mid-1980's and a declining level of abundance thereafter (Wilderbuer and Zhang, In press). The stock synthesis model estimates indicate that the population biomass increased steadily from 1971, peaking in 1984 at over 947,000 t. The population has been in decline since, and the biomass is currently estimated to be only 50% of the peak level. The biomass-based approach to cohort analysis similarly estimates a prolonged period of increasing biomass since 1971 peaking in 1988 at 850,000 t and declining thereafter to 50% of the maximum level by 1995. Compared to the biomass-based cohort analysis model, synthesis estimates suggest a higher biomass from 1971 to 1987. The two models show close agreement for 1987-93.

The annual bottom trawl survey estimates indicate an increase in biomass from 1975 through 1984 and a stable trend during 1985–97 at levels ranging from 515,000 t to 700,000 t (Table 9). Due to the large amount of variability associated with the trawl survey point estimates, the trawl surveys do not detect the declining trend in the population biomass since the mid-1980's estimated by the two age-structured models.

Recruitment Strengths

Estimates of age 6 recruitment from the two age-structured models corroborate the observed population increase and subsequent decline during a period

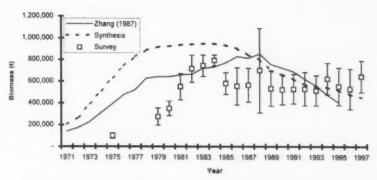


Figure 9.—Biomass estimates for eastern Bering Sea Alaska plaice from biomass-based cohort analysis, stock synthesis, and annual bottom trawl surveys.

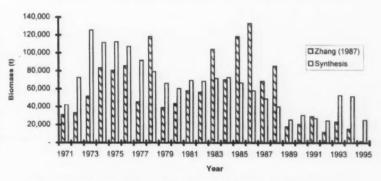


Figure 10.—Year-class strength at age 6 for Alaska plaice as estimated by biomass-based cohort analysis and stock synthesis.

Table 9.—Estimated biomass and 95% confidence intervals of Alaska plaice from U.S. bottom trawl surveys in 1975 and 1979–97.

Year	Biomass (t)	95% Confidence intervals
1975	103,500	82,989-124,105
1979	277,200	191,893-362,504
1980	354,000	288,224-423,706
1981	535,800	409,912-661,742
1982	715,400	587,034-843,783
1983	743,000	614,060-871,887
1984	789,200	560,625-1,017,735
1985	580,000	457,966-701,990
1986	553,900	383,587-724,212
1987	564,400	409,133-719,572
1988	699,400	309,641-1,089,139
1989	534,000	372,787-695,183
1990	522,800	386,807-658,775
1991	529,100	393,436-664,703
1992	530,400	378,004-682,871
1993	515,200	377,428-652,954
1994	623,100	479,130-767,028
1995	552,300	380,524-724,060
1996	529,300	344,200-714,400
1997	643,400	498,000-788,300

of light exploitation (Fig. 10). Estimates since 1989 suggest a lack of good recruitment relative to the consistently strong recruitment estimated from the

1970's and 1980's which provided the population increase. Synthesis model recruitment estimates from the 1971–77 period were higher than those from the biomass-based model, resulting in the higher biomass estimates observed in the 1970's and early 1980's (Fig. 9). The population has declined as the large year classes, which recruited at age 6 prior to 1988, are now older than the age where they maximize their cohort biomass. The lack of recruitment to the fishable biomass in subsequent years has contributed to the population decline.

Current Management and Estimation of Yield

Maximum Sustainable Yield

Estimates of MSY are 54,300 t based on the biomass-based production model. The stock biomass that would provide this long-term yield (B_{MSY}) is

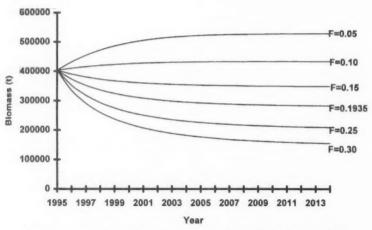


Figure 11.—Projections of estimated biomass for Alaska plaice from 1995 to 2014 using Zhang's difference equation under different harvest strategies.

estimated at 280,000 t, well below the current biomass estimate of over 400,000 t. The instantaneous rate of fishing mortality for MSY (F_{MSY}) was estimated at 0.194, much higher than the average F of less than 0.05 since 1971.

ABC for 1998

Alaska plaice of the eastern Bering Sea are managed under the jurisdiction of the North Pacific Fishery Management Council (NPFMC). Each year the NPFMC determines the total allowable catch (catch quota) for each management species derived from the Acceptable Biological Catch (ABC). The ABC currently used is based on Amendment 44 to the fisheries management plans for the Bering Sea/Aleutian Islands region and the Gulf of Alaska. These regulations set ABC commensurate upon the amount of reliable information available for the current biomass, the management parameters B_{MSY} , F_{MSY} , $F_{0.30}$, and $F_{0.40}$ and the relationship between the current biomass and B_{MSY} (Clark,

The ABC for the 1998 fishing season, according to present management guidelines, can be calculated with the following considerations. Since reliable estimates of initial 1998 biomass, B_{MSY} , F_{MSY} , $F_{0.35}$, and $F_{0.40}$ exist and the stock size at the beginning of 1998 is projected to be about 430,000 t (which is above B_{MSY}) using F levels for 1996 and

1997 of 0.05, ABC can be calculated as follows:

$$ABC = F_{MSY}B_{98}\frac{1}{Z}(1-e^{-z}),$$

where B_{98} is the initial 1998 biomass estimated by the projection of the biomass-based approach to the production model, $F_{MSY} = 0.194$, and natural mortality = 0.2. This results in an ABC = 68,900 t which is higher than MSY (54,300 t) since the stock condition is presently above B_{MSY} .

Biomass Projections

Alaska plaice biomass through the year 2025 was projected using the biomass-based approach to the production model for six different F regimes ranging from 0.05–0.30 (Fig. 11). Under the optimum F level (F_{MSY} = 0.194) the biomass was projected to remain stable at 280,000 t (B_{MSY}). Biomass levels as low as 200,000 t could be reached within 7 years at a fishing mortality of 0.30 in the projection. If future harvest levels remain at current levels, the stock biomass should vary with recruitment success, as in past years.

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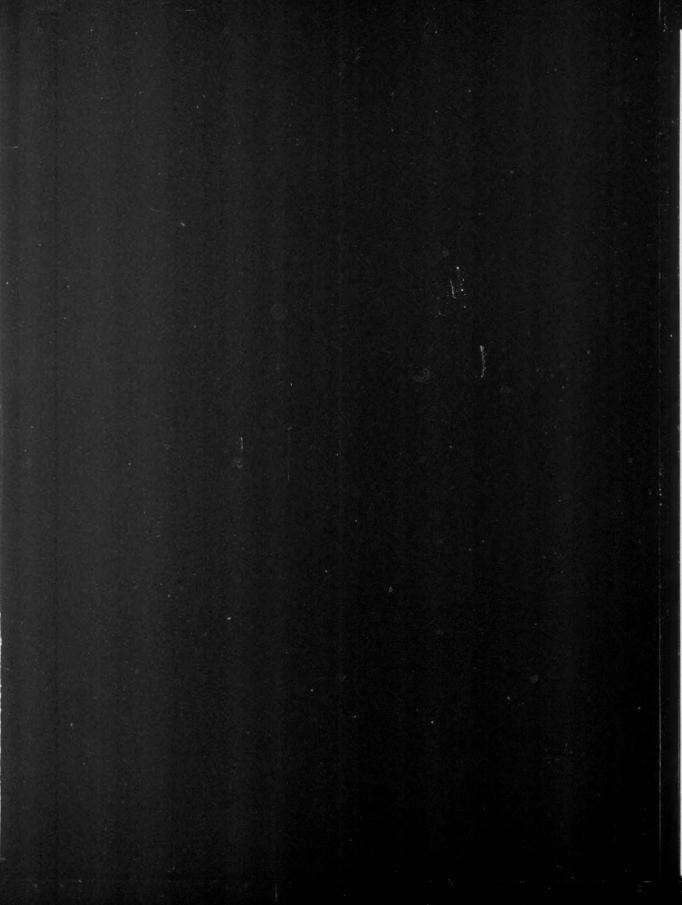
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Keep titles, heading, subheadings, and the abstract short and clear. Abstracts should be short (one-half page or less) and double-spaced. Paper titles should be no longer than 60 characters; a four- to five-word (40 to 45 characters) title is ideal. Use heads sparingly, if at all. Heads should contain only 2-5 words; do not stack heads of different sizes.

Style

In style, the Marine Fisheries Review follows the "U.S. Government Printing Office Style Manual." Fish names follow the American Fisheries Society's Special Publication No. 12, "A List of Common and Scientific Names of Fishes from the United States and Canada," fourth edition, 1980. The "Merriam-Webster Third New International Dictionary" is used as the authority for correct spelling and word division. Only journal titles and scientific names (genera and species) should be italicized (underscored). Dates should be written as 3 November 1976. In text, literature is cited as Lynn and Reid (1968) or as (Lynn and Reid, 1968). Common abbreviations and symbols such as mm, m, g, ml, mg, and °C (without periods) may be used with numerals. Measurements are preferred in metric units; other equivalent units (i.e., fathoms, °F) may also be listed in parentheses.

Tables and Footnotes

Tables and footnotes should be typed separately and double-spaced. Tables should be numbered and referenced in text. Table headings and format should be consistent: do not use vertical rules.

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Title the list of references "Literature Cited" and include only published works or those actually in press. Citations must contain the complete title of the work, inclusive pagination, full journal title, and the year, month, volume, and issue numbers of the publication. Unpublished reports or manuscripts and personal communications must be footnoted. Include the title, author, pagination of the manuscript or report, and the address where it is on file. For personal communications, list the name, affiliation, and address of the communicator.

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All figures should be clearly identified with the author's name and figure number, if used. Figure legends should be brief and a copy may be taped to the back of the figure. Figures may or may not be numbered. Do not write on the back of photographs. Photographs should be black and white, 8 × 10 inches, sharply focused glossies of strong contrast. Potential cover photos are welcome, but their return cannot be guaranteed. Magnification listed for photomicrographs must match the figure submitted (a scale bar may be preferred).

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